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COMPARISON OF AGE AT SEXUAL MATURITY FOR TWO STOCKS OF OFFSHORE SPOTTED DOLPHINS SUBJECTED TO DIFFERENT RATES OF EXPLOITATION

By

S.J. Chivers and A.C. Myrick, Jr.

ADMINISTRATIVE REPORT LJ-91-31

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Comparison of age at sexual maturity for two stocks of offshore spotted dolphins subjected to different rates of exploitation

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ABSTRACT

We examined the average age at attainment of sexual maturity (ASM) and associated reproductive parameters for evidence of density compensatory responses in two recognized stocks of the spotted dolphin, Stenella attenuata. The northern and southern stocks were compared because they have both been reduced in abundance. Consequently, decreasing trends in ASM and increasing trends in pregnancy rate were predicted for each stock. A lower ASM and higher pregnancy rate were predicted for the northern stock because this stock is more depleted. No statistically significant temporal trends were detected, but the mean parameter estimates were contrary to our predictions and imply a lower reproductive rate for the northern stock. The ASM was significantly different between the stocks: 11.12 years (SE = 0.229) for the northern stock and 9.78 years (SE = 0.264) for southern stock. The pregnancy rates, though not significantly different, were 0.27 and 0.34 for the northern and southern stocks, respectively. The observed results suggest that the populations are not responding in a straight-forward way to increases in per-capita availability of resources. Possible additional explanations may include (1) stock differences, (2) non-linear dynamics of population compensatory responses, (3) physiological stress, or (4) changes in carrying capacity.

INTRODUCTION

The use of biological parameters as possible correlates to population abundance has been investigated for a number of large mammal populations (Nicholson 1933; Murdoch 1970; Royama 1977; Fowler 1987; McCullough 1990). As population abundance declines, one would expect to see increases in survival and pregnancy rates and a decrease in the average age at sexual maturity (ASM; Eberhardt 1977; Eberhardt and Siniff 1977). However, the pattern of compensatory responses is undoubtedly species specific (DeMaster 1984a; York 1987; Fowler 1988). The identification of biological indices for a species may provide a useful management

tool to monitor trends in population abundance (Hanks 1981; Gerrodette and DeMaster 1990).

Compared to r-selected species, large mammals and other K-selected species are expected to exhibit a muted population compensatory response, as population abundance changes, due to physiological constraints (e.g. delayed ASM and birth of a single or few young). Yet specific components of population growth rate may still be found to correlate with population density (Stubbs 1977; Fowler 1981; Goodman 1981; McCullough 1990). Environmental variability, parameter measurement error, magnitude of the maximum parameter response and range of densities over which measurements are made, are critical determinants of whether a response will be detected.

Maximal response for all parameters is expected to occur at high densities, within 20-40% of carrying capacity (K), for large mammals (Fowler 1981). For species that are difficult to observe, like the offshore spotted dolphin studied here, unbiased estimates of survival rates are difficult to obtain, precluding their use as potential biological indicators (Barlow and Boveng 1991). Reproductive rates, however, are generally more easily measured and may serve as indices of a compensatory response in a population (Perrin and Donovan 1984). For instance, Barlow (1985) reported that the fraction of mature females pregnant and the fraction simultaneously pregnant and lactating may be good indices of per capita resource availability for the spotted dolphin.

The offshore spotted dolphin is the primary dolphin species used as a cue by purse-seine vessel operators to find yellowfin tuna in the eastern tropical Pacific (ETP; Perrin 1969). Some dolphins are incidentally killed during fishery operations and the spotted dolphins have had the largest number of animals killed almost every year since 1959 (DeMaster et al. 1991). In the first decade of the purse-seine fishery, i.e., the 1960s, the large numbers of dolphins killed presumably resulted in a significant decline in population abundance. The northern offshore spotted dolphin was estimated to be between 35% and 50% of their pre-exploitation abundance (pre-1959) by 1979 (Smith 1983). The southern stock was estimated to be at 92-98% of pre-exploitation size in 1979, and available data indicate that this stock was virtually unexploited before 1973 (Smith 1979). Since the 1976, both stocks of spotted dolphin are believed to have declined significantly in abundance (Anganuzzi et al. 1991).

As a potential biological index of change in population abundance, we examined the ASM for the offshore spotted dolphin. Although for long-lived mammals, like the spotted dolphin, population growth rates are relatively insensitive to changes in ASM (Eberhardt and Siniff 1977; Fowler 1981; Reilly and Barlow 1986), this parameter has been correlated with changes in

population abundance for other marine mammal species. A decrease in ASM was correlated with a decline in population abundance for baleen whale stocks (Lockyer 1984). Similarly, a decrease in ASM for crabeater seals was correlated with an increase in the per capita availability of food resources resulting from the exploitation and subsequent reduction in the size of baleen whale stocks (Bengtson and Laws 1985). Likewise, the ASM for the striped dolphin of the western Pacific declined in response to exploitation and reduced population abundance (Kasuya 1985).

We proposed to determine the suitability of ASM as a biological index by testing for temporal trends in ASM in two declining stocks of spotted dolphin and by comparing the two stocks that have different histories of exploitation. The two stocks selected for comparison, the northern and southern offshore spotted dolphin, are morphologically distinct in body size, coloration, and skull characteristics (Perrin et al. 1985).

We predicted a decline in ASM for both the northern and southern stocks of offshore spotted dolphins after 1974 as well as a lower ASM for the relatively more exploited northern stock. Additionally, we predicted that a higher pregnancy rate and a higher fraction of females simultaneously pregnant and lactating would be observed for the northern stock, relative to the southern stock.

METHODS

Life history data were collected from all cetacean species incidentally killed in the ETP yellowfin tuna purse-seine fishery. The National Marine Fisheries Service (NMFS) first placed observers aboard U.S. vessels in 1968. Beginning in 1974, life history data collection procedures were standardized, and the original sampling scheme that selectively collected large, female specimens was replaced by a random sampling scheme that selected the first available individual dead dolphins brought aboard (Perrin and Oliver 1982). In 1979, the Inter-American Tropical Tuna Commission (IATTC) joined the NMFS in placing observers aboard U.S. vessels and collecting life history data.

Exploitation of the spotted dolphin has not been spatially uniform. The yellowfin tuna purse-seine fishery began primarily as a coastal fishery in 1959 and gradually expanded farther offshore. The Commission's Yellowfin Regulatory Area (CYRA) was established in 1968 by the IATTC and provides a useful boundary that separates the inshore fishery area from the westernmost region of the ETP yellowfin tuna fishery (Peterson and Bayliff 1985). The area west of the CYRA was not fished until the late-1960s, and the southern region of the fishery, south of the equator, was not fished until the early 1970s (Punsly 1983). The system for data collection had been established by the time the fishery extended into these areas.

The two stocks of offshore spotted dolphins are defined as being north or south of 1° south latitude. The sample for the southern stock was collected south of the dividing latitude. The northern stock sample, however, was restricted to those animals collected north of 1° south and west of the CYRA boundary, approximately west of 120° west latitude (Fig. 1). Evidence for seasonal movement of spotted dolphins along the 10° north latitude as well as from the south to the west does exist (Perrin et al. 1979a; Au and Perryman 1985; Reilly 1990), but due to the large size of the area, interchange between the inshore and offshore animals and the northern and southern animals is probably limited. Given this history, the selection of these two distinct geographic regions, provides us our best opportunity for testing potential biological indices because in the southern and western part of the fishery the beginning of data collection is most likely to correspond with the time period when compensatory responses would be expected.

Female offshore spotted dolphins with complete life history data (i.e. geographic position, total body length, teeth collected and both ovaries examined), collected between 1974 and 1988, were randomly selected for this study. Fifty specimens per year were selected or, if fewer specimens were available, all for that year were prepared. Due to the relative paucity of specimens collected from the southern stock, all available specimens were prepared. Thin sections of the teeth were prepared and aged by one of us (ACM) using the techniques described in Myrick et al. (1983). Prior to estimating age, the prepared sample, all specimens were numerically coded to disguise the specimen number so that no inference could be made about the stock or collection year for any specimen. All age estimates were made without knowledge of the associated life history data for the specimen.

Data on sample size and precision for estimating ASM were available from a study reported by Hohn (1989), and using this information we decided that 50 specimens per year would be adequate for detecting a 1.5 year change in ASM over an 18 year period, 1971-88. We considered a 1.5 year change to be biologically realistic. Methods described in Gerrodette (1987) were used to determine the detectability of a change over time given a 6% coefficient of variation for estimates of ASM, an 18-year time series of data, $\alpha = 0.05$ and $\beta = 0.10$.

ASM is calculated as the sum of the fraction of sexually immature animals in the indeterminate age classes (i.e. age classes with both sexually immature and sexually mature animals), added to the age of the first indeterminate age class. The variance calculated for the estimates is the sum of the binomial variances for each indeterminate age class (DeMaster 1984b; Hohn 1989). A simple linear regression was used to test for temporal trends.

The other reproductive parameters examined include the fraction of the females mature, and the fraction of mature females that were pregnant, lactating and simultaneously pregnant and lactating. Trends in these parameters were examined with a chi-square test for linear trends (Snedecor and Cochran 1973).

RESULTS

Average age at attainment of sexual maturity

ASM was estimated for each year with sufficient available data. For the northern stock, ASM estimates were made for each year, 1973, 1976-1982 and 1984-1988 (n = 546), and the regression line fit to these data was not significantly different from zero. The only years with adequate sample sizes for estimating ASM for the southern stock were 1976, 1979 and 1982 (n = 319), and therefore, we did not fit a regression line to these data (Fig. 2). The data were then pooled for all years, and the estimate of ASM was 11.12 years (SE = 0.229) for the northern spotted dolphin and 9.78 years (SE = 0.264) for the southern spotted dolphin. This difference in ASM was statistically significant ($t=14.32$, $df=13$, $p< 0.001$).

The range in age of animals attaining sexual maturity was largest for the northern stock. The youngest mature animal was 7 years, and the oldest immature was 16 years. The same range for the southern stock was 6 to 11 years. The age distributions for the northern and southern stocks were compared, and the age distribution for immature animals was found to be significantly different ($p < 0.0001$) while the age distribution of mature animals was only marginally significantly different ($p = 0.055$) between the stocks using a Kolmogorov-Smirnov two-sample test (Siegel 1956). The difference in ASM between the two stocks is due to the different ranges in age at attainment of sexual maturity and the sample distributions.

For completeness, we also calculated average length at sexual maturity (LSM) and asymptotic length for each stock from this data set. We calculated LSM using the same method that we had used to estimate ASM. The estimate of LSM for the northern stock sample was 177.5 cm (SE = 0.565) and for the southern stock sample was 175.0 cm (SE = 0.572). Asymptotic length was estimated as the length of the 99th percentile of the length frequency distribution (Barlow and Boveng 1991) and was 205 cm for the northern stock and 199 cm for the southern stock. The estimate of asymptotic length for the northern stock was longer than the 190 cm that was estimated from the asymptote of a fitted growth curve (Perrin et al. 1976). No comparable estimate for the southern stock was available.

Reproductive rates

The corresponding non-age-specific reproductive data were examined for these same data. Linear trends in the proportion of the sample sexually mature and the proportion of mature females pregnant, lactating and simultaneously pregnant and lactating were tested for slopes significantly different from zero over the study period: 1974-1988. The only significant trends were an increase in the proportion of mature females simultaneously pregnant and lactating in the northern stock, indicating a compensatory response, and a decrease in the proportion of mature specimens in the sample from the southern stock. The data for all years were pooled and no significant differences were detected between the northern and southern stocks in any of the parameters (Table 1). Although not significantly different (Chi-square = 3.25, df = 1, p = 0.07), the pregnancy rate was 0.27 for the northern stock and was 0.34 for southern stock; the opposite direction to that predicted for a compensatory response.

DISCUSSION

The mean life history parameters for the northern stock (high ASM and low percent pregnant) imply a lower reproductive rate, relative to the southern stock. Due to the greater rate of exploitation of the northern stock of spotted dolphins, these patterns were predicted to be the opposite to what we observed. The only parameter that exhibited the predicted trend was the proportion of mature females simultaneously pregnant and lactating; a significant increase in this proportion was detected for the northern stock. The lack of consistent evidence for compensatory responses led us to examine other possible explanations for what we observed.

Initially, the model of population compensation that we used as a framework to posit our hypotheses made several implicit assumptions, including: (1) constant data collection biases, (2) minimal interchange of animals between areas, (3) consistent estimation of specimen age, (4) linear compensatory response with change in population abundance, (5) constant carrying capacity, and (6) equivalent initial life history parameters for the two stocks. The fact that we did not observe the predicted compensatory responses may be because (1) too few data were available, (2) parameter measurements were in error, (3) there was an unaccounted for time lag, or (4) no changes occurred in the range of observed population abundance. Each of these assumptions and potential problems are discussed in turn.

First, the possible problems in detecting compensatory responses will be discussed. Data for the southern stock of spotted dolphins, in particular, were limited and precluded

testing for a trend over the study period. Our results indicate that larger sample sizes would be required to detect small, but biologically significant, changes in the parameters we examined. We found that the 50 specimens per year that we had reasoned would be an adequate sample size, resulted in too few specimens in the indeterminate age classes used to estimate ASM. Perhaps a sample of 50 specimens in the indeterminate age classes would be more appropriate. Errors in the estimation of parameters as a result of sampling bias or too few samples may increase variability, and thus, reduce the ability to detect differences (Goodman 1984). Environmental periodicity (e.g. El Nino) may also increase variability in parameters and influence the detectability of compensatory mechanisms. Time lags may also be a factor in detecting compensatory responses. A time lag due to the late age at which animals reach sexually maturity and the multi-year breeding cycle characteristic of the spotted dolphin and many other cetacean species would be expected.

The first 3 of the 6 assumptions we made for testing the proposed hypotheses are believed to hold reasonably well. Barlow (1985) reported that several of the life history parameters examined were relatively insensitive to a number of potential data collection biases and no major changes in the collection of life history data were made after 1974, thus supporting constant data collection bias as a reasonable assumption. Geographic variability has been noted in earlier studies of spotted dolphin life history data (Hohn and Hammond 1985; Barlow 1985), thus selecting specimens from discrete areas as we did, reduces the potential for geographic variability to obscure population compensatory responses. Similarly, estimating the age of all specimens at one time and in the blind, ensured that the age estimates were made as consistently as possible.

Another concern when analyzing data that are collected from a kill is whether the age distribution is representative of the population. All immature age classes appear to be underrepresented in both stocks, and between 10 and 15 years there appears to be a further under-representation in the age distribution of the northern stock (Fig. 3). This phenomenon was noted in a previous aging study of ETP spotted dolphins but occurred about 5 year classes earlier than we observed (Barlow and Hohn 1984). This difference may be a result of different readers estimating age (ACM and another reader made age estimates for specimens in the earlier sample). The underrepresentation of these age classes may be a result of segregation in the population by age and sex, fairly typical in large mammal populations, and may affect the estimation of ASM. We investigated the effect of this underrepresentation by assuming a stable age distribution and apportioning the animals in the indeterminate age classes by sexual maturity under different assumptions for the sexual maturity of the animals in those age classes, and then calculating ASM. On the basis of segregation

by age and sex observed in other species of large mammals, we predicted that the most reasonable scenario for reconstructing the age distribution, is that the "missing" animals would be sexually immature. If this indeed were the case, we have underestimated ASM. Under this and the other scenarios we investigated, estimates of ASM were consistently over- or underestimated. Therefore, possible sampling biases are unlikely to be responsible for the observed differences in ASM.

Our results appear to be substantiated but are still contrary to our predictions. This may be interpreted as evidence that additional factors are contributing to population regulation or that population regulation is not occurring. Possible explanations of our results include (1) inherent stock differences, (2) non-linear dynamics of population compensatory responses, (3) physiological stress, and (4) changes in carrying capacity. Each possibility is discussed in turn.

Stock Differences

One of the initial assumptions made in designing this experiment to evaluate ASM as a biological index was that the life history characteristics of the north and south were equivalent prior to the perturbation of the purse-seine fishery. However, there may be inherent differences between the northern and southern stocks of spotted dolphin as a result of genetic divergence or of differences in their environments. Morphologically the two stocks are recognized as distinct (Perrin et al. 1985). The animals from the northern stock are, on average, 2.5 cm longer as adults and have different body coloration and skull characteristics (Perrin et al. 1979b). The growth patterns of the two stocks, with the northern animals being shorter at birth and weaning but longer at sexual maturity and full adult growth, also may suggest separate stocks (Bright and Chivers 1991; Perrin et al. 1979b).

The breeding seasons are also different. In the north the breeding season is diffuse throughout the year although two peaks are apparent: March to June and September to November. Whereas, for the southern stock, there is a single, relatively distinct peak in the spring (March to June) with few births noted during the rest of the year (Barlow 1985). These patterns of reproductive seasonality are likely correlated with the different oceanographic environments: the north being more constant and the south more variable (Au and Perryman 1985; Reilly 1990). Although there is some evidence for movement of animals between populations, the data on distribution, morphology, and life history characteristics suggest that the northern and southern stocks of spotted dolphins are distinct biological populations. Thus, the observed difference in ASM between the northern and southern samples may reflect a stock difference.

Non-linear Dynamics of Population Compensatory Responses

As noted in the introduction, the population of northern offshore spotted dolphins declined markedly during the 1960s and 1970s. More recent estimates of abundance indicate that during the period of data collection by observers on tuna vessels, there has been a further decline in abundance of spotted dolphins, at least through the 1970s and early 1980s (Anganuzzi et al. 1991). The more recent decline in abundance has been less dramatic than the initial decline that reduced the northern population to between 35% and 50% of K by 1979 (Smith 1983). The theorized dynamics of change in survival and reproductive rates for large mammals is that changes are nonlinear and that the largest changes occur between 20% and 40% below K (Fowler 1981). For this reason, the maximum compensatory responses were expected to have occurred during the first decade of the fishery. If this is the case, our results are not surprising as no change in ASM or other biological parameters would be expected over the observed range of population densities for the northern stock. While the southern stock abundance estimates suggest that the stock was within the range where compensatory responses might be detected, our sample sizes may have been too small.

Physiological stress

The stress imposed by the chase and ensuing encirclement of the dolphin schools may affect the animals physiologically. The characteristics of the ETP yellowfin tuna purse-seine fishery are unlikely to allow the dolphins to adequately compensate for the stress by altering their behavior, and thus, physiological changes would be expected. The result of change in an individual animal's physiological condition may be to reduce their ability to withstand disease, reproduce or grow. Through these mechanisms, physiological stress may contribute to population regulation (Christian and Davis 1964). Indices that reflect stress have been sought to monitor population condition, although they have proved difficult to define and measure (Hanks 1981; Moberg 1987). Current research has focused on investigating measures of physiological processes in several populations as correlates of environmental stress (e.g. Harlow et al. 1987; Myrick 1988; Smith and Bubenik 1990; Miller et al. 1991).

If stress in the environment is a significant factor, a straight-forward population compensatory response model would not predict the appropriate responses. There may be no changes in biological parameters, or negative compensation may occur, with changes occurring in the opposite direction to what would normally be expected (i.e. growth and reproductive rates would decrease, not increase). This is because biological resources would have to be diverted to help the animal cope with the stress

(Moberg 1987). An additional factor that may increase the significance of physiological stress on dolphins in the ETP is that as population abundance declines, the per capita exposure to the stressor (chase and encirclement) increases. This may be an explanation for the higher ASM and lower pregnancy rate we observed for the northern stock, if we assume equal initial values for both stocks. The smaller length-at-birth of northern stock animals from the same geographic area as our selected study area would also fit this pattern of negative compensation. The longer total adult length of the northern stock animals does not fit with this pattern, but the higher ASM would allow a longer time to get to the greater length as the growth rates between the two stocks are equal (Bright and Chivers 1991).

The ASM estimates for both the northern and southern stock animals are relatively high for delphinid species but they are within the range of published estimates. The range of age estimates for female delphinids becoming sexually mature from 4 years to 14 years with a mean of 8.4 years (Perrin and Reilly 1984). The previously published estimate of ASM for the northern stock of spotted dolphin is 11.4 years (Myrick et al. 1986) which closely corresponds to our estimate of 11.1 years. The estimate for spotted dolphins from the western Pacific is 9 years, and the range in ages of animals reaching sexual maturity is 7.5 years to 11.5 years of age (Kasuya 1976). The less exploited southern stock animals from the ETP and the population in the western Pacific appear to be similar in their age parameters, but inferences made by comparison to other studies must be made carefully as different researchers use different techniques. For instance, Kasuya (1976) estimated ASM by determining the age at which 50% of the animals were mature from a linear regression fit to the data whereas other researchers use a logistic model (Jorgensen 1981) or the summation method that we used. Another area of concern when comparing studies is the interpretation of annual layering patterns by different readers (Bryden 1986; Hohn 1990).

Changes in the range of ages that mammalian species become mature has been correlated with resource availability and may also be influenced by the rate of exploitation. Kasuya (1985) presented such an explanation for the decrease in the minimum age of spotted dolphins collected in sampled drive fishery catches. ASM and the range in age at attainment of sexual maturity was correlated with physiological, nutritive or social stresses in three different East African elephant populations. The population with the oldest maturing females was in the least favorable environment (Laws and Parker 1968). Thus, supporting the idea that the greater range in age at sexual maturity observed for the northern stock of the spotted dolphin is a result of the stress imposed by the fishery on that population.

We posit two hypotheses to compare reproductive rates

between the northern and southern stocks that are likely to change as a result of physiological stress (Moberg 1987). First, we hypothesize that there would be more corpora atretica (i.e. ovarian scars that indicate an unsuccessful ovulation [Perrin et al. 1976; Marsh and Kasuya 1984; Perrin and Donovan 1984]) accumulating with age in animals from the northern stock, and second, that the average number of age-specific ovulation scars would be lower in the sample for the northern stock than in the sample for the southern stock. The expected response for each of these hypotheses assumes that physiological stress is most severe for the northern stock as a result of the northern animals being exploitated by the fishery for a longer period of time and the northern stock being reduced in abundance farther below K than in the south. The age distributions of mature specimens for the northern and southern stock are not statistically different and this allows us to make the necessary assumption of equal rates of corpora atretica scar disappearance for the two stocks to test the first hypothesis. The accumulation of atretic corpora by age class was tested with a Wilcoxin signed-rank test and were not significantly different between the northern and southern stocks. Using the same statistical test, we found that the mean number of total corpora (excluding corpora atretica) in each age class was not significantly different between the two stocks.

Changes in Carrying Capacity

Although assumed to be constant, carrying capacity may have changed since 1959 when the purse-seine fishery began to exploit the dolphin populations. Changes in K may be due to changes in environmental productivity or, perhaps more likely, to niche replacement. A change in K would likely change the per capita availability of resources, and hence, compensatory responses would occur. There is no current information to test for a change in K but the possibility of a change cannot be dismissed.

Concluding Remarks

Given the caveats, the population compensatory model that we used to predict changes in biological parameters as per capita resources increased, may not be sufficient to explain the observed data. Inherent biological differences between the northern and southern stocks are a possible explanation and will be further investigated. Another explanation is that repeated purse-seine sets are likely to impose significant physiological stress. One of us (ACM) is developing a theoretical model to describe how physiological stress may alter a variety of growth and reproductive responses in cetaceans.

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TABLE

Table 1. The following reproductive parameters are summarized: proportion of mature females in the female sample and the proportion of mature females that are pregnant, lactating and simultaneously pregnant and lactating. The estimates were made for each stock with years pooled. The number of females in the sample from the northern stock was 563 and from the southern stock, 392. As a subset of this sample, there were 347 mature females in the northern stock sample and 263 from the southern stock sample.

Parameter	Stock	
	North	South
Mature	0.63	0.69
Pregnant	0.27	0.34
Lactating	0.50	0.42
Pregnant and Lactating	0.06	0.06

FIGURES

Figure 1. The geographic distribution of our sample. The sample sizes were summed by 2°-degree square block. The sample of northern spotted dolphins was selected from north of the equator and west of the Commission's Yellowfin Regulatory Area (the dashed line), and the sample of southern spotted dolphins was from south of the equator.

Figure 2. Estimates of ASM by stock for the offshore spotted dolphin with 1 SE. If no SE bar was plotted, then there were no overlapping indeterminate age classes. Solid circles represent estimates of ASM for the northern stock and open triangles for the southern stock. The pooled estimate of ASM for the northern stock (N) is 11.12 years (dashed line) and 9.78 years (dashed and dotted line) for the southern stock (S). The sample sizes for each year with an estimate of ASM available are printed to the right of the data point. The number of animals in the indeterminate age classes was a subset of the total sample for the year and ranged from 8 to 18 for the northern stock sample and 11 to 24 for the southern stock sample.

Figure 3. Age frequency distribution for the sample of northern and southern stocks of offshore spotted dolphins.

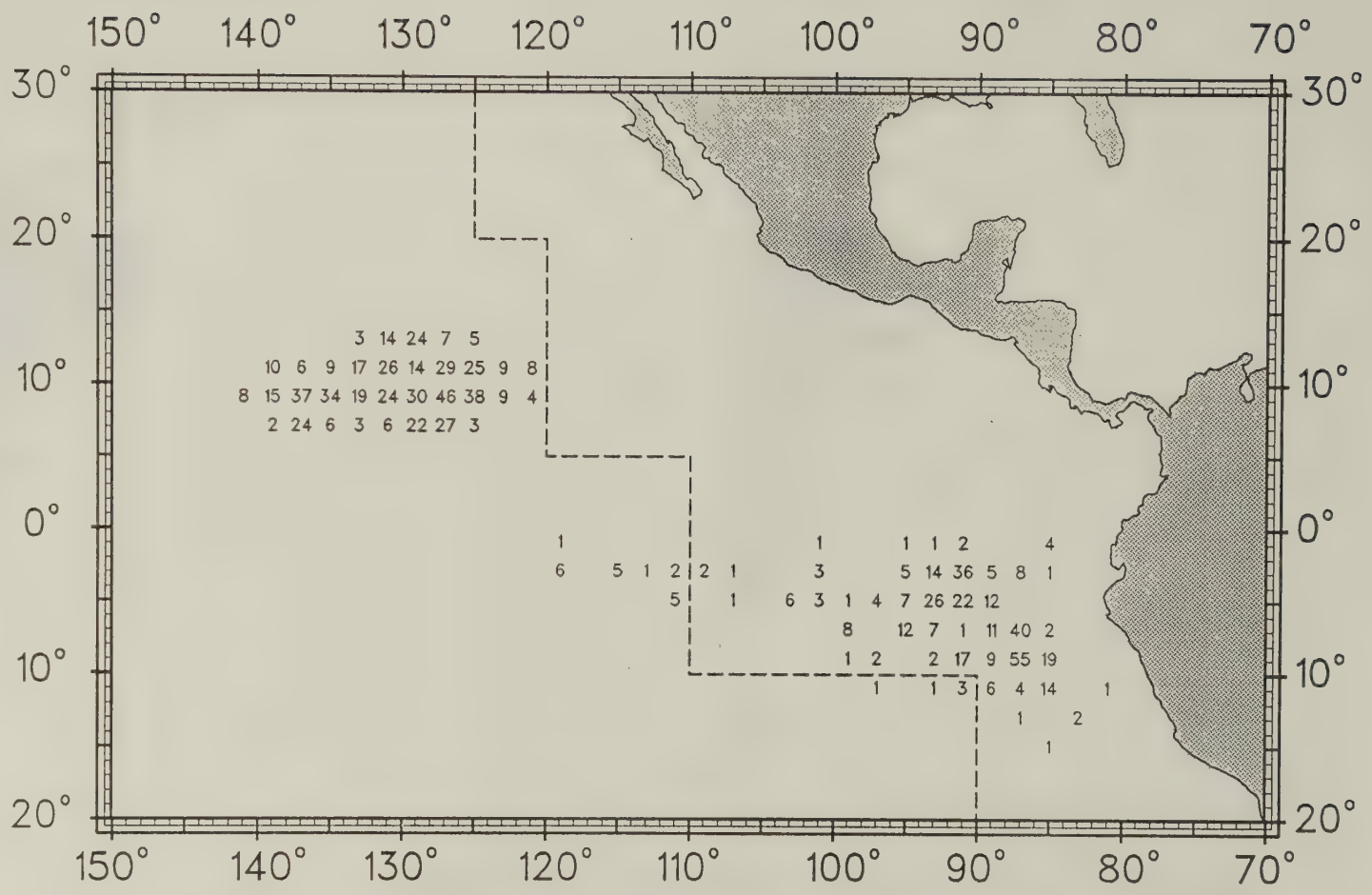

150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° 10° 20°
3 14 24 7 5
10 6 9 17 26 14 29 25 9 8
8 15 37 34 19 24 30 46 38 9 4
2 24 6 3 6 22 27 3
1
6 5 1 2
5
2 1
1
1
3
6 3 1 4 7 26 22 12
8 12 7 1 11 40 2
1 2 2 17 9 55 19
1 1 3 6 4 14 1
1 2
1
1 1 2 4
5 14 36 5 8 1

Fig. 1

FIG. 2.

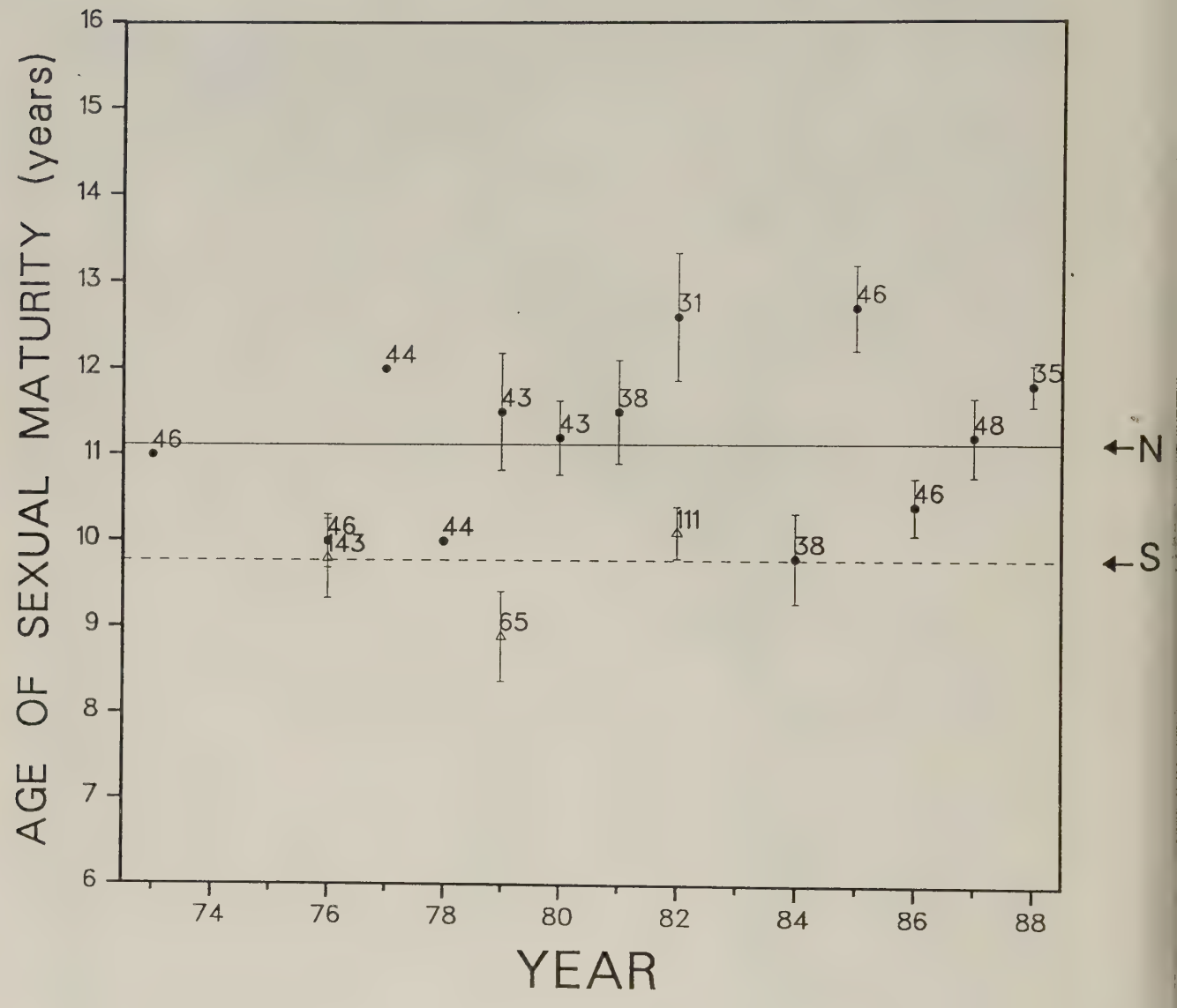
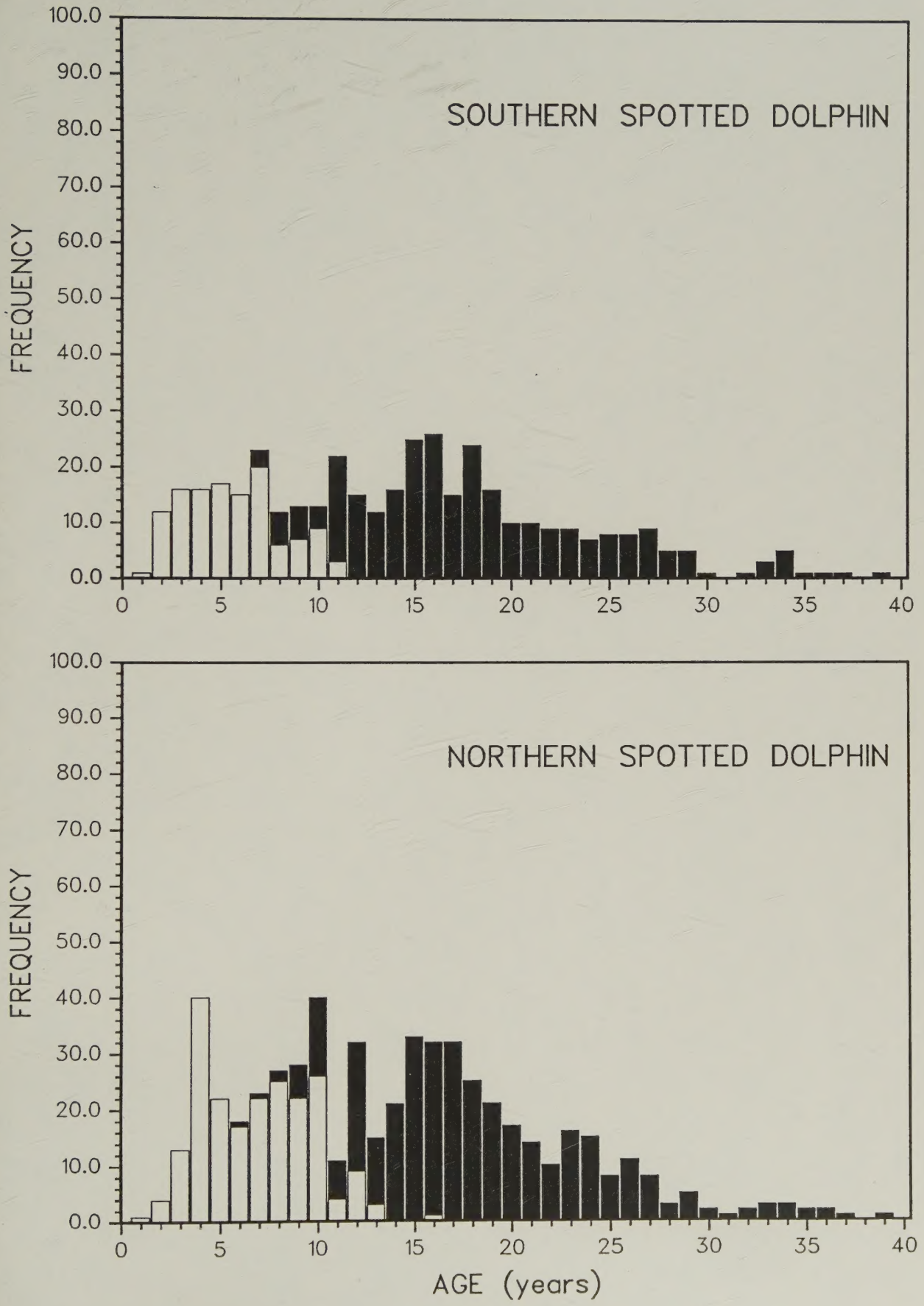

AGE OF SEXUAL MATURITY (years)
16
15
14
13
12
11
10
9
8
7
6
74
76
78
80
82
84
86
88
YEAR
46
44
43
43
38
31
46
35
48
46
46
43
44
111
38
65
N
S

FIG. 3.


SOUTHERN SPOTTED DOLPHIN
NORTHERN SPOTTED DOLPHIN
FREQUENCY
FREQUENCY
100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
0
5
10
15
20
25
30
35
40
AGE (years)